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TAXONOMY OF *VACCINIUM* SECTION *OXYCOCCOIDES* (ERICACEAE)

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ABSTRACT

The Appalachian *Vaccinium erythrocarpum* and the SE Asian *V. japonicum* are morphologically indistinct and share a similar chromosome number ($n = 12$). Their flavonoid profiles are also quite similar; however, the two taxa do show some difference in their capacity to accumulate derivatives of the two flavonols kaempferol and quercetin: *V. japonicum* accumulates both, while *V. erythrocarpum* accumulates only quercetin. Reciprocal crossing experiments between the taxa produce fertile hybrids. Therefore in the absence of a potential genetic barrier and no morphological gap, the reduction of these vicariads to subspecies is warranted. Consequently *V. erythrocarpum* subspecies *japonicum, comb. et stat. nov.* is proposed.

Key Words: *Vaccinium, Oxycoccoides,* taxonomy, flavonols, chromosome numbers, southeast Asia, southeast U.S.

INTRODUCTION

Taxa referred to *Vaccinium* section *Oxycoccoides* (Hooker f.) Sleumer share the following features: perennating buds covered by two partially fused prophylls; solitary flowers borne in leaf axils and set on nodding pedicels continuous with the calyx tube; corolla deeply 4-cleft; stamens eight, thecae awnless with long, slender tubules. Berry 4-locular, with each locule containing 20–25 ovules.

Currently section *Oxycoccoides* is comprised of two disjunct species, *Vaccinium erythrocarpum* Michx., a local endemic in the Appalachians of the southeastern U.S. (Wood, 1961; Vander Kloet, 1988) and *V. japonicum* Miq., widely distributed in the highlands of southern China, Formosa and Japan (Wood, 1961; Horikawa, 1972; Fang, 1986). *Vaccinium japonicum* consists of three varieties (Wood, 1961): var. *sinicum* (Nakai) Rehd. is restricted to China (Fang, 1986), var. *lasiostemon* Hayata to Formosa, and var. *japonicum* to Japan and Quelpaert Island (Wood, 1961). The only morphological difference between these vicariads is that the Appalachian material is usually somewhat more glandular-pubescent and robust than the Asian (Table 1; Sleumer, 1941; Vander Kloet, 1988). These differences are scarcely sufficient to warrant specific status, especially when one considers that *V.*

Table 1. Morphological comparison between selected attributes of the North American *Vaccinium erythrocarpum* and the Asian *V. japonicum*. Values given are means ± one standard deviation.

Character	*V. erythrocarpum*	*V. japonicum*
1. Plant height	30–150 (200) cm	(10) 20–60 (150)
2. Habit	rhizomatous (crown-forming)	rhizomatous (crown-forming)
3. Twigs	± terete	± terete
4. Twig indumentum	pubescent in lines	glabrous to pubescent
5. Leaf: width	23 ± 5 mm	19 ± 3 mm
6. Leaf: length	53 ± 10 mm	41 ± 9 mm
7. Leaf: margin	serrate	serrate
8. Leaf: blade	glandular beneath	± eglandular beneath
9. Corolla lobes	reflexed at anthesis	reflexed at anthesis
10. Filaments	pilose	pilose
11. Anther sac tubules	4 ± 1 mm long	4 ± 1 mm long
12. Pedicel length	8–15 mm	10–20 mm
13. Berry color	red, deep purple, black	red

japonicum var. *ciliare* Matsumura was established to accommodate the more glandular and pubescent Japanese material. Before combining these highly disjunct populations into a single species, however, their karyology, flavonoid chemistry, and ecology are described in some detail to evaluate their status.

MATERIALS AND METHODS

Collection data for the population samples analyzed are given in Table 2. In addition to leaf and twig collections, 20 to 30 ripe berries were also collected at each site. Berries were measured to the nearest millimeter. Seeds were washed from the berries, air dried, and the large, plump, brown seeds were separated from the small, pale or collapsed ones, and each batch was counted. From the plump seeds, 10 were randomly selected and weighed individually to .001 g on a Cahn Model 4100 electronic balance. Means and standard deviations were calculated for the seeds from each accession number and expressed as mg/100 seeds.

The seeds were either stored in sealed jars at 2°C for at least 6 months and then placed in pots on a 1:1 peat-sand mixture in a misting chamber in the greenhouse or germinated fresh on a 1:1 peat-sand mixture in a misting chamber. Stored seeds were germinated under 14 hours of light at 28 ± 5°C and 10 hours of

Table 2. Collection data for *Vaccinium* section *Oxycoccoides*. 1 = seed collections for crossability studies; 2 = analyzed for flavonoid constituents; 3 = chromosomes counted. msm = *meters supra mare* = meters above sea level.

V. erythrocarpum Michx. U.S.A. North Carolina: Avery Co.: Grandfather Mt. at 1100 msm. *Vander Kloet 134877* (1, 2); Haywood Co.: Water-rock Knob at 1462 msm. *Vander Kloet 11981, 21981* (1, 2, 3); Gaylord Stoney Tennent Mt. at 1510 msm. *Vander Kloet 61981, 71981, 81981* (1, 2, 3); Blue Ridge Parkway at Richland Balsam Gap, 1512 msm. *Vander Kloet 41981, 51981* (1, 2, 3).
V. japonicus Miq. JAPAN. Nagans Prefecture: Bandokoro, Minamia zumi-gun, 1300 msm. *Vander Kloet 218886* (2); Gifu Prefecture: Takayama, 919-7 Jwaicho, 1300 msm. *Vander Kloet 125886* (1, 2, 3); Mt. Sanpo-i-wa, 1200–1445 msm. *Vander Kloet 225856* (3); Kyoto Prefecture: Midorogaike pond, Sakyo-ku, Kyoto, 100 msm. *Vander Kloet 126886, 226886* (1, 2, 3).

darkness at 13 ± 2°C. Fresh seeds were germinated under a similar regime or at temperatures of 22 ± 3°C/5 ± 2°C. When the cotyledons emerged, pots were removed from the misting chamber, placed on greenhouse benches and watered daily, if necessary. Days to emergence of radicles, of cotyledons and of first leaves, and percent germination were recorded. Three months after germination, five or more vigorous seedlings were pricked off; each was set out in a 10 cm clay pot, and watered when necessary.

In late summer of the following year, all plants were transferred to coldframes and kept there until the following spring when they were returned to the greenhouse for cytogenetic studies and crossing trials.

A series of young flower buds from each population was fixed, stained and squashed following the procedure of Hall and Galletta (1971) so that their chromosome numbers could be determined. Remaining flower buds were allowed to develop on the plants; anthesis began in about 3 weeks. Initially a few flowers were selfed on all plants; subsequently reciprocal outcrosses were attempted within and between Japanese and Appalachian plants. All selfs and outcrosses were tagged to follow ovule development. Once each berry was ripe, the seeds were removed, counted, and sown directly so that the viability of the progeny could be determined.

Dried leaves from the following sources were analyzed for flavonoids: herbarium specimens (listed in the appendix); dried specimens of wild populations; and fresh material from both garden- and greenhouse-grown plants, including some of the hybrids described below. Plants were extracted with 80% methanol by

soaking for several days. After a final wash with boiling 80% methanol, the extracts from individual plants were combined and evaporated to dryness under reduced pressure at 35°C; residues were then extracted with boiling water to remove their polar components. Extraction of the aqueous solutions with water-saturated n-butanol yielded the polyphenolic fractions. The n-butanol solutions were reduced to dryness under reduced pressure and the residues taken up in small volumes of methanol. The methanol solutions were applied to TLC plates (Polyamid 6.6, homemade) and chromatographed two-dimensionally in the solvent systems described by Wilkins and Bohm (1976). Spots were made visible by examination under UV light and by spraying with diphenylboric acid ethanolamine complex (.1% in 50% aqueous methanol) and examination under UV light. Identifications are based upon characteristic chromatographic and color behavior of the compounds involved using standards.

RESULTS

Chromosome counts were consistently diploid ($n = 12$). Thirty-four preparations were examined from which 11 clear counts were obtained, three from the Appalachians and eight from Japan. Morphology, length of the chromosome and genome sizes were quite similar to those described by Hall and Galletta (1971) for three other sections of *Vaccinium,* namely, sections *Cyanococcus* A. Gray, *Herpothamnus* (Small) Sleumer and *Oxycoccus* (Hill) Koch.

However, an error has crept into the literature. Bolkhovskikh et al. (1969), citing a report by Flory (1937) and repeated by Funabiki (1958), stated that *Hugeria japonica* (Miq.) Nakai, a synonym of *Vaccinium japonicum* Miq., has a diploid chromosome number of 14. But Flory (1937) reported only counts for the Polemoniaceae, not the Ericaceae, and this particular count refers to *Hugelia japonica* Benth. A recorded *lapsus linguae,* perhaps!

Selfing invariably failed, probably due to the same late acting incompatibility system that results in massive embryo abortion as has been reported by Vander Kloet (1991) for *V. corymbosum* L., but outcrossing was quite successful (Table 3). Seventy-five percent of the crosses attempted among the Appalachian plants were successful, producing 30 ± 11 seeds/berry; crosses among

Table 3. Comparative crossability between and among plants of *Vaccinium erythrocarpum* and *V. japonicum*. Values are means ± one standard deviation; data in parentheses from material collected in the wild.

Taxon	*V. erythrocarpum*		*V. erythrocarpum* × *V. japonicum*		*V. japonicum*	
Number of crosses	32		26		17	
Seed set (days)	59 ± 7		71 ± 10		58 ± 3	
Relative set success	75%		61%		86%	
First radicle emerges (days)	13 ± 1	(15 ± 1)	14 ± 1		18 ± 2	(16 ± 2)
First cotyledons (days)	24 ± 2	(24 ± 1)	25 ± 2		31 ± 4	(34 ± 6)
First true leaves (days)	33 ± 3	(34 ± 6)	35 ± 4		45 ± 5	(58 ± 10)
Seeds/berry	30 ± 11	(10 ± 7)	35 ± 8		35 ± 19	(24 ± 6)
Seed wt (mg/100 seeds)		(29 ± 10)				(23 ± 8)
Relative germination success	94%	(71%)	51%		80%	(14%)

the Japanese plants produced a similar number of seeds per berry, but berry set was 11% higher than in the Appalachian crosses. Similarly, crosses between these vicariads produced 35 ± 8 seeds/berry when fresh pollen was used. The use of pollen stored dry at −20°C for 6 months markedly reduced seed set (4 ± 5 seeds/berry). Storage was necessary because these vicariads display different phenologies in the Acadia greenhouse. The Japanese plants sometimes begin to bloom within a year after germinating and they continue to bloom sporadically throughout the year with only a minimal chilling period (about 20 hours at 0 to 2°C). The Appalachian plants, however, require about five years after germination before they will bloom; they also need eight months of chilling to break dormancy and then bloom only once for about three weeks in June. Nonetheless, the hybrids produced by crossing these disjunct taxa are as vigorous as plants from the intraspecific crosses and produce ample normal pollen which is indistinguishable from that of parental plants.

The lower seed set per berry observed in wild populations (Table 3) may be attributable to interflower selfing (Vander Kloet and Lyrene, 1987) and/or to few pollinators, since the floral display is never massive in these plants but rather diffuse and asynchronous. We have yet to observe an insect visit these flowers in the wild.

Seed germination and seedling development were quite good for all seed populations, both wild and greenhouse-grown, except for seed collected from *Vaccinium japonicum* in the wild (Table 3). The Japanese plants not only had berries that contained somewhat smaller seeds which weighed about 20% less than those of *V. erythrocarpum* (23 ± 8 mg/100 seeds for the former vs. 29 ± 10 mg/100 seeds for the latter), but these seeds also exhibited much poorer germination (14% success vs. 71% for *V. erythrocarpum*) and took longer to develop first true leaves as a seedling than *V. erythrocarpum* (58 ± 10 days vs. 34 ± 6 days). Even seed produced in the greenhouse from intraspecific crosses and which had much higher germination than the wild seed (80% vs. 14%) nevertheless took 12 days more to produce a seedling than *V. erythrocarpum*.

Some of these phenological differences in blooming, seed set and germination may be due to genetic drift since the populations are small and local, or to habitat selection against mesic forms in the Appalachians, or to a combination of both factors. *Vac-*

cinium japonicum occurs in mixed coniferous stands or beech forests from sea level to 2600 msm (*meters supra mare*) (Horikawa, 1972) while *V. erythrocarpum* occurs primarily in openings of red spruce, Fraser fir and yellow birch stands from 1500 to 1950 msm in the southern Appalachians (Busing et al., 1988).

The flavonoid profiles of the two species, and of their hybrids, are based upon the common flavonols kaempferol and quercetin in the form of their 3–0–glycosides, eriodictyol 7–0–glucoside and a variety of blue-fluorescing compounds that are likely derivatives of cinnamic acids.

The flavonoid pigment profiles for the two taxa show some difference in their capacities to accumulate derivatives of the two flavonols kaempferol and quercetin: *Vaccinium japonicum* accumulates both, while *V. erythrocarpum* accumulates only quercetin and its derivatives. The two taxa are further differentiated by the tendency of *V. japonicum* to make higher-order glycosides as well as monoglycosides, in contrast to the tendency of *V. erythrocarpum* to make principally monoglycosides.

Vaccinium erythrocarpum is characterized by comparatively large amounts of quercetin 3–0–glucoside (galactoside may also be present), 3–0–rhamnoside, 3–0–glucuronide and eriodictyol 7–0–glucoside. There were no kaempferol monoglycosides in this taxon and only faint traces of diglycosides in a few individuals. *Vaccinium japonicum,* on the other hand, exhibited both kaempferol and quercetin 3–0–monoglucosides (possibly galactosides as well) and 3–0–diglycosides. Likewise, a trace of quercetin 3–0–glucuronidae was indicated; eriodictyol 7–0–glucoside was present but not abundant.

The F_1 hybrids often (but not always) had complementary flavonoid profiles. This result was not entirely unexpected since some of the Japanese parents used in the crossing experiments were missing one or more flavonoids, such as eriodictyol 7–0–glucoside.

It is noteworthy that the variation observed in the flavonoid chemistry mimics the morphological variation. In SE Asia where the species is polymorphic, none of the plants had identical flavonoid profiles, but the monomorphic Appalachian plants all had similar flavonoid profiles.

All these data suggest that the Appalachian and the Asian taxa, although tertiary relicts *sensu* Wood (1972), are not distinct biological entities; indeed, the only qualitative difference observed

in this study was the presence of kaempferol monoglycoside in *Vaccinium japonicum* and its absence in *V. erythrocarpum*. The remainder of the morphological and biological evidence, such as the ability to interbreed with no apparent loss of fertility in the hybrids and only minor quantitative differences in morphology, supports the notion of a single species with several ecotypes or biotypes. Since these ecotypes are quite disjunct, it might be useful to recognize them at the sub-specific level.

TAXONOMIC TREATMENT

Vaccinium section **Oxycoccoides** Hooker f. in Benth. et Hook. f., Gen. Pl. 2: 573. 1876.

V. subgenus *Oxycoccoides* (Hook. f.) Sleumer, Nat. Bot. Gart. Mus. Berlin-Dahlem 13: 111. 1936.
Oxycoccoides (Hook. f.) Nakai, Bot. Mag. Tokyo 31: 246. 1917.
Hugeria Small, Fl. S.E. U.S. 896. 1336. 1903.

Shrubs up to 3 m tall; main growth of the plant carried out by shoots other than those that bear flowers; buds composed of 2 partially-fused prophylls; leaves deciduous; flowers solitary in leaf axils borne toward the ends of shoots of the same season, set on nodding pedicels continuous with the calyx tube. Corolla deeply cleft, 4-merous; stamens 8, exerted at anthesis, awnless, with long tubules. Berry 4-locular, each locule with 20–25 ovules.

Rehder (1927) reported that in section *Oxycoccoides,* the calyx tube is articulated with the pedicel; Sleumer (1941) observed that the berry is 5-loculed and the corolla 5-merous; Palser (1961) has stated that the stamens have short awns. We have been unable to verify any of these observations in the specimens collected in the field or examined at A, GH, K, BM and NY.

Stevens (Taxonomic studies in the Ericaceae. Ph.D. thesis, University of Edinburgh, 1969) has observed that in section *Oxycoccoides* there is extensive lignification around the midrib bundle.

Section *Oxycoccoides* has a southeastern North American and eastern Asian distribution, a pattern first detected and described by A. Gray in 1860 for some 150 taxa of flowering plants, and usually explained in terms of a distribution that became disrupted by climatic changes or by migration connected with these changes. Wood (1961) regarded this section as a morphological intermediate between section *Myrtillus* and section *Oxycoccus*. The for-

mer has similar perennating buds, bears single flowers in the axils of the lower leaves on the vegetative shoots, and the calyx tube is continuous with the pedicel; section *Myrtillus* differs from section *Oxycoccoides* in that the flowers are 5-merous, have 10 awned stamens, and the corolla lobes are not reflexed at anthesis. Section *Oxycoccus* has a 4-merous flower, eight awnless stamens, and corolla lobes deeply cleft at anthesis, but it differs from section *Oxycoccoides* in that the calyx tube is articulated with the pedicel, the pedicels bear bracts, and the inflorescence is frequently reduced into a pseudo-raceme (especially in *V. oxycoccus*) and the testa is more than a single layer of cells thick (Vander Kloet, 1983).

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V. japonicum Miq., Ann. Mus. Bot. Ludg.-Bat. 1: 28. 1863.
V. randaiense Hayata, J. Coll. Sci. Tokyo 30: 168. 1911.
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H. japonica (Miq.) Nakai in Nakai *et* Koidz., Trees and Shrubs Japan Proper (ed. 2) 227. 1927.
H. incisa F. Maekawa, Bot. Mag. Tokyo 47: 614. 1933.
H. lasiostemon (Hayata) Maekawa, Bot. Mag. Tokyo 47: 617. 1933.
H. randaiensis (Hayata) Masamune, J. Soc. Trop. Agric. Taiwan 4: 301. 1932.
H. sinica (Nakai) Maekawa, Bot. Mag. Tokyo 47: 615. 1933.
Oxycoccus erectus Pursh., Fl. Am. Sept. 1: 264. 1814.
O. japonicus (Miq.) Makino, Bot. Mag. Tokyo 18: 18. 1904.
O. erythrocarpus (Michx.) Persoon, Syn. 1: 419. 1805.
Oxycoccoides erythrocarpus (Michx.) Nakai, Bot. Mag. Tokyo 31: 247. 1917.
O. japonicus (Miq.) Nakai, Bot. Mag. Tokyo 31: 247. 1917.

KEY TO THE SUBSPECIES

A. Plants 60–150 cm high; leaves 53 ± 10 mm long; kaempferol monoglycoside absent; SE North America . . . . . *V. erythrocarpum*

AA. Plants 30–60 cm high; leaves 41 ± 9 mm long; kaempferol monoglycoside present; SE Asia . . . . . *V. japonicum*

Vaccinium erythrocarpum Michx. subspecies **erythrocarpum**

Shrubs (50) 80–150 (300) cm high, crown-forming or weakly rhizomatous; twigs of current season smooth, ± terete, pubescent

in lines; leaves elliptical, ovate to oblong-lanceolate, deciduous, membranaceous, 40–70 mm long, 15–30 mm wide, glandular-pubescent beneath, green on both sides, margin serrulate; calyx and pedicel continuous, glabrous, calyx lobes 4, <1 mm long, pedicel up to 1.5 cm long with a pair of caducous basal bracteoles; corolla lobes 4, deeply reflexed at anthesis, white, pink, rarely red; stamens with the filaments pilose, the anther sacs awnless, tubules 3–5 mm long; pollen tetrads 33–37 μm in diameter. Berry red, deep purple or black (*f. nigrum* Allard), (6) 9–11 (15) mm in diameter; nutlet ca. 1 mm long. Chromosome number $n = 12$.

TYPE LOCALITY. High Mountains in northern Carolina. TYPE at *P*. Lectotypified by Vander Kloet (1989).

RANGE. Southeastern North America in the Appalachians at high elevations from West Virginia to northern Georgia. Several outlying populations occur in central Tennessee (Vander Kloet, 1988).

HABITAT. Wooded slopes, subalpine shrubbery, boggy areas, rocky slopes and thickets from (600) 1000–1950 msm. In the southern Appalachians, subspecies *erythrocarpum* frequently occurs in virgin spruce-fir forests (Busing et al., 1988) where it is associated with *Viburnum alnifolium* Marsh., *Rubus canadensis* L., and *Sambucus pubens* Michx. (Oosting and Billings, 1951).

Vaccinium erythrocarpum Mich. subspecies **japonicum** (Miq.) Vander Kloet, *comb. et stat. nov.*

var. *fauriei* Sleumer, Bot. Jahrb. 71: 490. 1941.
var. *ciliare* Matsumura in Nakai, Trees and Shrubs of Japan 2: 229. 1927.
var. *sinicum* (Nakai) Rehder, J. Arnold Arbor. 5: 56. 1924.
var. *lasiostemon* Hayata, J. Coll. Sci. Imp. Univ. Tokyo 30: 449. 1911.

Shrubs (15) 30–60 (150) cm high, crown-forming or weakly rhizomatous; twigs of the current season ± terete, usually glabrous, occasionally pubescent; leaves 15–55 mm long, 10–30 mm wide, usually eglandular and glabrous beneath, rarely pubescent and glandular; leaves and pedicels of flowering shoots occasionally very much reduced; berries red, 5–7 (10) mm in diameter. Chromosome number $n = 12$.

Using pedicel length, leaf shape and leaf margin, as well as blade-petiole indumentum, Maekawa (1933) divided this SE Asian

population into four species. However, pedicel length is quite plastic, and consequently variation within a single clone is often of the same magnitude as that encountered between populations from different areas. This variation is especially true of those few plants that have pedicels which continue to elongate prior to, during, and after anthesis. The remaining diagnostic features cited by Maekawa are not constant and occur in various combinations. Whoever would accept two species here will eventually be led to accept four, then perhaps eight!

TYPE LOCALITY. Japan; TYPE at L! Von Siebold 102330. Herb. Ludg.-Bat 908. 265–275.

RANGE. Southeastern Asia; Japan; Quelpaert Island (Korea); Formosa (Taiwan) and southeastern China.

HABITAT. Coniferous woods, mixed coniferous woods, beech forests, subalpine shrubberies, sub-alpine grasslands, rocky slopes and thickets from sea level to 2500 msm.

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APPENDIX

Citation of herbarium specimens from which 3–6 leaves were removed so that their flavonoid constituents could be adduced.

U.S.A.: **Georgia,** Rabun County, 1951 *Duncan 12545* (ACAD); **Tennessee,** Sevier County, 1930 *Jennison S. M.* (GH); **West Virginia,** Munroe County, 1931 *Hunnewell 12018* (GH). JAPAN: **Uzen Province,** Hondo, 1914 *Wilson 7209* (A); **Aomori Prefecture,** Hakkodo, Yachionsen, 1976 *Yamazaki 1031* (A); **Isikawa Prefecture,** Yamanaka, Enuma-gun, 1955 *Muroi 23155* (A). CHINA: **Western Hupeh,** 1922 *Chun* (A); **Chekiang,** 1932 *Ho 1625* (A).